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This contribution is published to honor Dr. Amnon Freidberg, a scientist, a colleague and a friend, on the occasion of his 75th birthday.

The economic significance of the signal fly genus *Rivellia* Robineau-Desvoidy (Diptera: Platystomatidae)

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ABSTRACT

Knowledge of the biology of signal flies is inadequate and scattered, with that for the genus *Rivellia* being better than other genera, but yet still insufficiently documented. This paper draws together the collective information on the biology of *Rivellia*, especially since many species attack root nodules of legume crops around the world. The growing economic importance associated with this biology hinges on increased demands for legume crops, especially soy, which is not only used in human food supply, but also as stock feed that indirectly benefits the human food chain. At least 22 species of *Rivellia* are associated with root nodules of legumes, including 32 different plant species interactions and many more varieties among these. Of these, seven species impact on the soybean *Glycine max* (L.) Merrill trade, which amounts to a global production of nearly 350 million tonnes per annum, accounting for 56 % of worldwide oilseed production with a market value of in excess of USD48 billion. So significant is the pest association of one species, *R. quadrifasciata* (Macquart, 1835), that it is known as the Soybean Nodule Fly (SNF). Indications from species analysis in the USA are that *Rivellia* species associated with root nodules of legume crops have shifted from a primary indigenous meadow legume to the mono-cultured crop species.

KEYWORDS: Diptera, Platystomatidae, *Rivellia*, signal fly, Fabaceae, soybean, agricultural entomology, economic significance, pests, review.

INTRODUCTION

In general among the signal flies biological details and knowledge of the juvenile stages exist for few species, *Rivellia* Robineau-Desvoidy, 1830 being an exception in which in depth agricultural studies have been conduced. Even within *Rivellia*, however, data are sparse and restricted to only 13 species (Table 1), plus a few undetermined species, of a potential total of approximately 140 species worldwide. Notably, larvae are associated with the living and the decaying root nodules of nitrogen fixing Fabaceae (including soybean, various varieties of peanuts and ground nuts, pigeon pea, common pulse crops used as culinary beans and pasture legumes) and with the roots or flowers of other plants such as eggplant, sorghum, black locust and *Narcissus* (Table 2). This is of economic significance,

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Fig. 1: Adult female *Rivellia quadrifasciata* (Macquart, 1835), feeding on common ninebark flowers (*Physocarpus opulifolius* (L.) Maxim., 1879 (Rosaceae)) at the Riveredge Nature Center in Ozaukee County (southeastern Wisconsin, USA). Photo credit: Kate Redmond, UWM Field Station.

because pest induced stress was noted as a major component preventing increased soybean yield in the USA by Newsom (1983) by significantly reducing nitrogen fixation and C_2H_4 production (Hutchinson 1979). These effects are equally likely to so affect other legume crops. Occasionally, adults are found associated with leguminous ornamental species; for instance, Byun *et al.* (2001) noted *Rivellia nigroapicalis* Byun & Suh, 2001 on *Pueraria montana* (Lour.) Merr. in Korea.

One species, *R. quadrifasciata* (Macquart, 1835) (Fig. 1), has become associated with the vernacular name Soybean Root Nodule Fly (SNF, Koethe & van Duyn 1984), but it is by no means the only species to have evolved a taste for soybean root nodules. Indeed, this vernacular name and variations of it pre-existed in Japan prior to common publication in American literature. Sugiyama and Mochizuki (1949) mention "*daizu-kiiro-konryu-bae*" (=soybean yellow root nodule fly; Hara 1993) for *R. basilaris* (Weidemann, 1830) and "*daizu-konryu-bae*" (=soybean root nodule fly; Hara 1993) for *R. apicalis* Hendel, 1934.

Being a cosmopolitan genus, associated with equally widely distributed legumes crops, the literature on the biology of this genus are dispersed and sometimes difficult to locate, being published in localised newsletters and agricultural bulletins. This paper reviews the literature of this collective knowledge and emphasises the economic significance of the signal fly genus *Rivellia*.

BOTANICAL ASSOCIATIONS

Members of the genus *Rivellia* were first reported on agricultural crops by Hoffman (1938), who reared *R. basilaris* (Wiedemann, 1830) from the fruit of *Solanum melongena* L. (aubergine, brinjal, or eggplant) in Kangton in China, contrary to Lui

Table 1. *Rivellia* (Diptera: Platystomatidae) associations with host plants.

Pest species	Stage	Host	Location	Reference
R. alini Enderlein, 1937	L/A?	*Glycine max* (L.) Merrill (soybean)	Jeonju, Republic of Korea	Oh *et al*. 2017
R. angulata Hendel, 1914	L	*Vigna triloba* (weed legume)	ICRISAT Center, India	Sithanantham *et al*. 1981
	L	*Cajanus cajan* (L.) Millsp. (pigeon pea, or red gram)	ICRISAT Center, India	Sithanantham *et al*. 1981, 1987; Kumar Rao & Sithanantham 1989; Reed *et al*. 1989
	L, A	*Cajanus cajan* (L.) Millsp. (pigeon pea, or red gram)	Greenhouse, Canada	Nambiar *et al.* 1990
	L	*Sorgorum bicolor* L. Moench (sorghum)	ICRISAT Center, India	Kumar Rao & Sithanantham 1989
R. apicalis Hendel, 1934	E, L, P, A	*Glycine max* (L.) Merrill (soybean)	Hokuriku, Japan	Sugiyama & Mochizuki 1949, 1950 (identified as *R. apicalis* by Koizumi 1957)
	L	*Glycine max* (L.) Merrill (soybean)	Hokkaido and Kyushyu, Japan	Koizumi 1957; Kobayashi 1981
	A	Honeydew on *Glycine max* (L.) Merrill (soybean)	Hokkaido and Kyushyu, Japan	Koizumi 1957
	L	Honeydew on *Glycine max* (L.) Merrill (soybean)	Sapporo, Japan	Kurosawa & Matsumoto 1961
	L	*Vigna angularis* (Willd.) Ohwi & H. Ohashi (Azuki bean and common bean plants such as scarlet runner)	Yarnanashi Prefecture, Japan	Suzuki & Mori 1963
	L/A?	*Glycine max* (L.) Merrill (soybean)	Jeonju, Republic of Korea	Oh *et al*. 2017

Table 1. *Rivellia* (Diptera: Platystomatidae) associations with host plants.

Pest species	Stage	Host	Location	Reference
R. basilaris (Wiedemann, 1830)	L	*Glycine max* (L.) Merrill (soybean)	Hokuriku, Japan	Sugiyama & Mochizuki 1949, 1950 (identified as *R. basilaris* by Koizumi 1957)
	L	*Glycine max* (L.) Merrill (soybean)	Hokkaido and Kyushyu, Japan	Koizumi 1957; Kobayashi 1981
	A	*Glycine max* (L.) Merrill (soybean)	Nagano and Osaka prefectures, Japan	Hara 1993
	L, A	Soybean (assumed to be *Glycine max*)	Shenzhen, China	Liu 2017
	L, A	Honeydew on *Glycine max* (L.) Merrill (soybean)	Hokkaido and Kyushyu, Japan	Koizumi 1957
	L	*Solanum nigrum* L. (hound berry, or nightshade)	Kwantung (today's Hebei Province) in China	Hoffman 1938
	L	*Solanum melongena* L. (aubergine, brinjal, or eggplant)	Kangton in China	Reported by Koizumi 1957
R. nr. *basilaris*	L	*Glycine max* (L.) Merrill (soybean)	Australia and New Zealand	Kogan *et al*. 1997
R. boscii Robineau-Desvoidy, 1830	L/A?	*Glycine max* (L.) Merrill (soybean)	Missouri, USA	Blickenstaff & Huggans 1962
R. flavimana Loew, 1873	L, P, A	*Amphicarpaea bracteata* (L.) Fernald (hog peanut)	USA	Namba 1956; Foote 1985; Foote *et al*. 1987
R. flavipes Hara, 1994	A	*Lespedeza bicolor* Turcz. (bush clover)	Hokkaido, Japan	Hara 1994

Table 1. *Rivellia* (Diptera: Platystomatidae) associations with host plants.

Pest species	Stage	Host	Location	Reference
R. flaviventris Hendel, 1914	A	*Vigna angularis* (Willd.) Ohwi & H. Ohashi (Azuki bean and common bean plants such as scarlet runner)	Nagano and Osaka prefectures, Japan	Hara 1993
	L/A?	*Glycine max* (L.) Merrill (soybean)	Jeonju, Republic of Korea	Oh *et al.* 2017
R. mandschurica Hennig, 1945	A	*Amphicarpaea bracteata* (L.) Fernald subsp. *edgeworthii* (Benth.) Ohashi var. *japonica* (Oliver) Ohashi (hog peanut)	Hokkaido, Japan	Hara 1994
	A	*Maackia amurensis* Rurp. & Maxim. var. *buergeri* (Maxim.) C.K. Schn. (Amur maackia)	Hokkaido, Japan	Hara 1994
	A	*Pueraria lobata* (Willd.) Ohwi (kudzu vine, or East Asian arrowroot)	Hokkaido, Japan	Hara 1994
R. melliginis (Fitch, 1855)	E, L, A	*Robinia pseudoacacia* L. (black locust tree)	USA	Namba 1956; Newson 1983; Foote 1985; Foote *et al.*1987; McMichael *et al.* 1990
R. metallica (van der Wulp, 1867)	A	*Amphicarpaea bracteata* (L.) Fernald (hog peanut)	USA	Namba 1956; Foote 1985; Foote *et al.* 1987
R. micans Loew, 1873	A	*Amorpha fruticosa* L. (false-indigo, or bush-indigo)	Oklahoma and Ohio, USA	Foote *et al.* 1987
R. munda Namba, 1956	A	*Amorpha fruticosa* L. false-indigo, or bush-indigo)	Oklahoma, USA	Foote *et al.* 1987

Table 1. *Rivellia* (Diptera: Platystomatidae) associations with host plants.

Pest species	Stage	Host	Location	Reference
R. nigricans Matsumura, 1916	L	*Glycine max* (L.) Merrill (soybean)	Hokkaido, Sapporo, Japan	Kurosawa & Matsumoto 1961; Hara 1994
	A	*Amphicarpaea bracteata* (L.) Fernald subsp. *edgeworthii* (Benth.) Ohashi var. *japonica* (Oliver) Ohashi (hog peanut)	Hokkaido, Japan	Hara 1994
	A	*Maackia amurensis* Rurp. & Maxim. var. *buergeri* (Maxim.) C.K. Schn. (Amur maackia)	Hokkaido, Japan	Hara 1994
	A	*Pueraria lobata* (Willd.) Ohwi (kudzu vine, or East Asian arrowroot)	Hokkaido and Honshu, Japan	Hara 1994
R. nigroapicalis Byun & Suh, 2001	A	*Pueraria montana* (Lour.) Merr. (kudzu, or Japanese arrowroot)	Korea	Byun *et al.* 2001
R. pallida Loew, 1873	E, L, P, A	*Amphicarpaea bracteata* (L.) Fernald (hog peanut)	USA	Namba 1956; Foote 1985; Bibro & Foote 1986; Foote *et al*. 1987
R. quadrifasciata (Macquart, 1835) Soybean Nodule Fly	L/A?	*Glycine max* (L.) Merrill (soybean)	Missouri, USA	Blickenstaff & Huggans 1962
	L	*Desmodium* spp. (trefoil)	USA	Foote 1985; Foote *et al*., 1987
	E, L, P, A	*Glycine max* (L.) Merrill (soybean)	Louisiana, USA	Eastman & Wuensche 1977; Hutchinson 1979
	L	*Glycine max* (L.) Merrill (soybean)	Louisiana, USA	Newsom *et al.* 1978

Table 1. *Rivellia* (Diptera: Platystomatidae) associations with host plants.

Pest species	Stage	Host	Location	Reference
R. quadrifasciata (Macquart, 1835) Soybean Nodule Fly	E, L, A	*Glycine max* (L.) Merrill (soybean)	USA	Koethe & van Duyn 1984
	L	*Glycine max* (L.) Merrill (soybean)	USA	Koethe & van Duyn 1985; Foote 1985; Koethe *et al.* 1986; Kohn 1990
	A	*Glycine max* (L.) Merrill (soybean)	USA	Koethe & van Duyn 1989
	L	*Phaseolus limensis* Macf. (lima beans)	USA	Koethe & van Duyn 1988
	E, L, A	*Vigna unguiculata* (L.) Walp. (brown-eyed crowder southern peas)	USA	Koethe & van Duyn 1984
	A?	*Chamaecrista fasciculata* (Michx.) Greene	Illinois, USA	Hilty 2015
	A?	*Strophostyles helvola* (L.) Elliott	Illinois, USA	Hilty 2015
R. steyskali Namba, 1956	L, A	*Desmodium paniculatum* L. (panicled tick-trefoil)	Ohio, USA	Foote 1985; Foote *et al.* 1987
R. variabilis Loew, 1873	L, P, A	*Apios americana* Medic. (potato bean, or groundnut)	Ohio, USA	Foote *et al.* 1987
R. viridulans Robineau-Desvoidy, 1830	E, L, P, A	*Robinia pseudoacacia* (black locust tree)	USA	Blanton 1938; Foote 1985; Foote *et al*. 1987
	L	*Narcissus* (rotting bulbs)	USA	Blanton 1938

Table 1. *Rivellia* (Diptera: Platystomatidae) associations with host plants.

Pest species	Stage	Host	Location	Reference
R. winifredae Namba, 1956	L, A	*Apios americana* Medikus (potato bean, or groundnut)	Northeast Ohio, USA	Namba 1956; Foote 1985
Rivellia sp.	L, A	*Arachis hypogaea* L. (peanut)	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
	L	*Cajanus cajan* (L.) Millsp. (pigeon pea, or red gram)	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980; Sithanantham *et al*. 1981
	L	*Crotalaria longithyrsa* Baker f.	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
	L	*Glycine max* (L.) Merrill (soybean)	Ina, Nagano Prefecture, Japan	Chiku & Miyashita 1957
	L	*Glycine max* (L.) Merrill (soybean)	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
	L	*Glycine max* (L.) Merrill (soybean)	Sapporo, Japan	Kurosawa & Matsumoto 1961
	L	*Glycine javanica* Thunb. H. (pasture legume)	Australia	Diatloff 1965
	L	*Phaseolus aureus* (mung bean)	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960

Table 1. *Rivellia* (Diptera: Platystomatidae) associations with host plants.

Pest species	Stage	Host	Location	Reference
Rivellia sp.	L	*Phaseolus mungo* (urd bean)	ICRISAT Center, Northern Karnataka, India	Sithanantham *et al*. 1981
	L	*Phaseolus radiatus* (mung bean)	ICRISAT Center, Northern Karnataka, India	Sithanantham *et al*. 1981
	L	*Vigna* (mung bean)	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980
	L	*Vigna radiata* (urd)	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980
	L	*Vigna sinensis* (cow pea)	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
	L	*Vigna unguiculata* (cowpea)	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980; Sithanantham *et al.* 1981
	L	*Voandzeia subterraneana* (Bambarra groundnut)	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
	L	groundnut	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980

(2017), who proposed it was newly introduced to China in 2016. In the same year as Hoffman, the horticultural association was made between adults on *Robinia pseudoacacia* L. (black locust tree) and on nearby rotting *Narcissus* bulbs in the USA (Blanton 1938). Such associations with non-legume hosts have not been noted since, suggesting *Rivellia* has a minor role as a pest in these host plants or that such information, being of no agricultural significance failed to be published.

Conversely, the role of members of *Rivellia* as a pest of legume crops is demonstrated by numerous field experiments, trials, reports and papers, beginning as early as 1949 on soybean (*Glycine max* (L.) Merrill) in Hokuriku, Japan (Sugiyama & Mochizuki 1949, 1950). Further early reports came from soybean and other crops in Yangambi, Democratic Republic of the Congo (Seeger & Maldague 1960); pasture legume (*Glycine javanica* Thunb. H.) in Australia (Diatloff 1965); various host plant associations in North America (Namba 1956); and on pigeon pea or red gram (*Cajanus cajan* (L.) Millsp.) in Northern Karnataka, India (Siddappaji & Gowda 1980). Many of these papers lead to the initiation of multiple experimental trials and assessments across the globe, underpinned by taxonomic revision in North America (Namba 1956).

Research in the USA focussed primarily on *R. quadrifasciata*, first recorded attacking soybean root nodules by Eastman and Wuensche (1977) and given the vernacular epithet Soybean Nodule Fly (SNF) by Koethe and van Duyn (1984). Koethe (1982) and Koethe & van Duyn (1984) demonstrated a significant association between adult fly emergence and root nodulation.

Considered to be of economic importance by Newsom (1983), *R. quadrifasciata* was later listed among the important soybean pests by Kogan *et al.* (1997). *R. quadrifasciata* was rated with a Pest Impact Rating (PIR, ranging 1(low) – 4(high)) of 2 (Sinclair *et al.* 1997), but the relevance of these ratings is entirely regional and dependent upon reported frequencies of insecticide application, such that a species such as *Heliothis armigera* (Lepidoptera: Noctuidae) has a PRI = 1 in Australia and New Zealand, but a PRI = 3 in India. On the other hand, Kogan and Kuhlman (1982) reported that although *R. quadrifasciata* was present in Illinois, the amount of nodule damage caused was probably insignificant.

In contrast, *Rivellia apicalis* Hendel, 1934 was not listed among the most important soybean pests in Japan by Kobayashi (1981), receiving only a single mention in the overall list of 241 species (belonging to 65 families in 9 orders) found to attack soybean, of which as few as 13 were Diptera, even though it is a pest of as broad a spectrum of legumes as *R. quadrifasciata* and is mentioned by as many authors in as many papers.

Foote *et al*. (1987) suggested that *R. quadrifasciata* had shifted from a natural legume host, such as tick trefoil (*Desmodium* sp.) to soybean. Adults were observed sucking nectar from *Strophostyles helvola* (L.) Elliott according to Hilty (2015). As indicated in Foote *et al.* (1987) and in Table 1, most of the secondary host plants are legumes, suggesting that natural legumes are probably the natural hosts for many members of *Rivellia*. Foote *et al.* (1987) further pointed that within

Table 2. Plant associations with *Rivellia* (Diptera: Platystomatidae).

Host	Pest species	Stage	Location	Reference
Amorpha fruticosa L. (false-indigo, or bush-indigo)	*R. micans* Loew, 1873	A	Oklahoma and Ohio, USA	Foote *et al.* 1987
	R. munda Namba, 1956	A	Oklahoma, USA	Foote *et al.* 1987
*Amphicarpaea bracteat*a (L.) Fernald (hog peanut)	*R. flavimana* Loew, 1873	L, P, A	USA	Namba 1956; Foote 1985; Foote *et al.* 1987
	R. metallica (van der Wulp, 1867)	A	USA	Namba 1956; Foote 1985; Foote *et al.* 1987
	R. pallida Loew, 1873	E, L, P, A	USA	Namba 1956; Foote 1985; Bibro & Foote 1986; Foote *et al.* 1987
Amphicarpaea bracteata (L.) Fernald subsp. *edgeworthii* (Benth.) Ohashi var. *japonica* (Oliver) Ohashi (hog peanut)	*R. mandschurica* Hennig, 1945	A	Hokkaido, Japan	Hara 1994
	R. nigricans Matsumura, 1916	A	Hokkaido, Japan	Hara 1994
Apios americana Medic. (potato bean, or groundnut)	*R. variabilis* Loew, 1873	L, P, A	Ohio, USA	Foote *et al.* 1987
	R. winifredae Namba, 1956	L, A	Northeast Ohio, USA	Namba 1956; Foote 1985
Arachis hypogaea L. (peanut)	*Rivellia* sp.	L, A	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960

Table 2. Plant associations with *Rivellia* (Diptera: Platystomatidae).

Host	Pest species	Stage	Location	Reference
Cajanus cajan (L.) Millsp. (pigeon pea, or red gram)	*R. angulata* Hendel, 1914	L	ICRISAT Center, Northern Karnataka, India	Sithanantham *et al.* 1981, 1987; Kumar Rao & Sithanantham 1989; Reed *et al.* 1989
	Rivellia sp.	L	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980; Sithanantham *et al.* 1981
Chamaecrista fasciculata (Michx.) Greene	*R. quadrifasciata* (Macquart, 1835) Soybean Nodule Fly	A?	Illinois, USA	Hilty 2015
Crotalaria longithyrsa Baker f.	*Rivellia* sp.	L	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
Desmodium paniculatum L. (panicled tick-trefoil)	*R. steyskali* Namba, 1956	L, A	Ohio, USA	Foote 1985; Foote *et al.*1987
Desmodium spp. (trefoil)	*R. quadrifasciata* (Macquart, 1835) Soybean Nodule Fly	L	USA	Foote 1985; Foote *et al.* 1987
Glycine javanica Thunb. H. (pasture legume)	*Rivellia* sp.	L	Australia	Diatloff 1965
Glycine max (L.) Merrill (soybean)	*R. alini* Enderlein, 1937	L/A?	Jeonju, Republic of Korea	Oh *et al.* 2017
	R. apicalis Hendel, 1934	E, L, P, A	Hokuriku, Japan	Sugiyama & Mochizuki 1949, 1950 (identified as *R. apicalis* by Koizumi 1957)

Table 2. Plant associations with *Rivellia* (Diptera: Platystomatidae).

Host	Pest species	Stage	Location	Reference
Glycine max (L.) Merrill (soybean)	*R. apicalis* Hendel, 1934	L	Hokkaido and Kyushyu, Japan	Koizumi 1957; Kobayashi 1981
	R. apicalis Hendel, 1934	L/A?	Jeonju, Republic of Korea	Oh *et al*. 2017
	R. basilaris (Wiedemann, 1830)	L	Hokuriku, Japan	Sugiyama & Mochizuki 1949, 1950 (identified as *R. basilaris* by Koizumi 1957)
	R. basilaris (Wiedemann, 1830)	L	Hokkaido and Kyushyu, Japan	Koizumi 1957; Kobayashi 1981
	R. basilaris (Wiedemann, 1830)	A	Nagano and Osaka prefectures, Japan	Hara 1993
	R. basilaris (Wiedemann, 1830)	L, A	Shenzhen, China	Liu 2017
	R. nr. *basilaris*	L	Australia and New Zealand	Kogan *et al*. 1997
	R. boscii Robineau-Desvoidy, 1830	L/A?	Missouri, USA	Blickenstaff & Huggans 1962
	R. flaviventris Hendel, 1914	L/A?	Jeonju, Republic of Korea	Oh *et al*. 2017
	R. nigricans Matsumura, 1916	L A	Hokkaido and Sapporo, Japan	Kurosawa & Matsumoto 1961; Hara 1994

Table 2. Plant associations with *Rivellia* (Diptera: Platystomatidae).

Host	Pest species	Stage	Location	Reference
Glycine max (L.) Merrill (soybean)	*R. quadrifasciata* (Macquart, 1835) Soybean Nodule Fly	L/A?	Missouri, USA	Blickenstaff & Huggans 1962
	R. quadrifasciata (Macquart, 1835)	E, L, P, A	Louisiana, USA	Eastman & Wuensche 1977; Hutchinson 1979
	R. quadrifasciata (Macquart, 1835)	L	Louisiana, USA	Newsom *et al.* 1978
	R. quadrifasciata (Macquart, 1835)	E, L, A	USA	Koethe & van Duyn 1984;
	R. quadrifasciata (Macquart, 1835)	L	USA	Koethe & van Duyn 1985; Foote 1985; Koethe *et al.* 1986; Kohn 1990
	R. quadrifasciata (Macquart, 1835)	A	USA	Koethe & van Duyn 1989
	Rivellia sp.	L	Ina, Nagano Prefecture, Japan	Chiku & Miyashita 1957
	Rivellia sp.	L	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
	Rivellia sp.	L	Sapporo, Japan	Kurosawa & Matsumoto 1961

Table 2. Plant associations with *Rivellia* (Diptera: Platystomatidae).

Host	Pest species	Stage	Location	Reference
Groundnut	*Rivellia* sp.	L	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980
Honeydew on *Glycine max* (L.) Merrill (soybean)	*R. apicalis* Hendel, 1934	A	Hokkaido and Kyushyu, Japan	Koizumi 1957
	R. apicalis Hendel, 1934	L	Sopporo, Japan	Kurosawa & Matsumoto 1961
	R. basilaris (Wiedemann, 1830)	L, A	Hokkaido and Kyushyu, Japan	Koizumi 1957
Lespedeza bicolor Turcz. (bush clover)	*R. flavipes* Hara, 1994	A	Hokkaido, Japan	Hara 1994
Maackia amurensis Rurp. & Maxim. var. *buergeri* (Maxim.) C.K. Schn. (Amur maackia)	*R. mandschurica* Hennig, 1945	A	Hokkaido, Japan	Hara 1994
	R. nigricans Matsumura, 1916	A	Hokkaido and Honshu, Japan	Hara 1994
Narcissus (rotting bulbs)	*R. viridulans* Robineau-Desvoidy, 1830	L	USA	Blanton 1938
Phaseolus aureus (mung bean)	*Rivellia* sp.	L	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
Phaseolus limensis Macf. (lima beans)	*R. quadrifasciata* (Macquart, 1835) Soybean Nodule Fly	L	USA	Koethe & van Duyn 1988
Phaseolus mungo (urd bean)	*Rivellia* sp.	L	ICRISAT Center, Northern Karnataka, India	Sithanantham *et al*. 1981

Table 2. Plant associations with *Rivellia* (Diptera: Platystomatidae).

Host	Pest species	Stage	Location	Reference
Phaseolus radiatus (mung bean)	*Rivellia* sp.	L	ICRISAT Center, Northern Karnataka, India	Sithanantham *et al*. 1981
Pueraria lobata (Willd.) Ohwi (kudzu vine, or East Asian arrowroot)	*R. mandschurica* Hennig, 1945	A	Hokkaido, Japan	Hara 1994
	R. nigricans Matsumura, 1916	A	Hokkaido and Honshu, Japan	Hara 1994
Pueraria montana (Lour.) Merr. (kudzu, or Japanese arrowroot)	*R. nigroapicalis* Byun & Suh, 2001	A	Korea	Byun *et al*. (2001)
Robinia pseudoacacia L. (black locust tree)	*R. melliginis* (Fitch, 1855)	E, L, A	USA	Namba 1956; Newson 1983; Foote 1985; Foote *et al*.1987; McMichael *et al.* 1990
	R. viridulans Robineau-Desvoidy, 1830	E, L, P, A	USA	Blanton 1938; Foote 1985; Foote *et al*. 1987
Sorgorum bicolor L. Moench (sorghum)	*R. angulata* Hendel, 1914	L	ICRISAT Center, India	Kumar Rao & Sithanantham 1989
Solanum melongena L. (aubergine, brinjal, or eggplant)	*R. basilaris* (Wiedemann, 1830)	L	Kangton in China	Koizumi 1957
Solanum nigrum L. (hound berry, or nightshade)	*R. basilaris* (Wiedemann, 1830)	L	Kwantung (today's Hebei province) in China	Hoffman 1938
Strophostyles helvola (L.) Elliott	*R. quadrifasciata* (Macquart, 1835) Soybean Nodule Fly	A?	Illinois, USA	Hilty 2015

Table 2. Plant associations with *Rivellia* (Diptera: Platystomatidae).

Host	Pest species	Stage	Location	Reference
Vigna angularis (Willd.) Ohwi & H. Ohashi (Azuki bean and common bean plants such as scarlet runner)	*R. apicalis* Hendel, 1934	L	Yarnanashi Prefecture, Japan	Suzuki & Mori 1963
	R. flaviventris Hendel, 1914	A	Nagano and Osaka prefectures, Japan	Hara 1993
Vigna radiata (urd)	*Rivellia* sp.	L	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980
Vigna sinensis (cow pea)	*Rivellia* sp.	L	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960
Vigna triloba (weed legume)	*R. angulata* Hendel, 1914	L	ICRISAT Center, India	Sithanantham *et al*. 1981
	R. angulata Hendel, 1914	L, A	Greenhouse, Canada	Nambiar *et al.* 1990
Vigna unguiculata (L.) Walp., (brown-eyed crowder southern peas)	*R. quadrifasciata* (Macquart, 1835) Soybean Nodule Fly	E, L, A	USA	Koethe & van Duyn 1984
	Rivellia sp.	L	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980; Sithanantham *et al.* 1981
Vigna (mung bean)	*Rivellia* sp.	L	ICRISAT Center, Northern Karnataka, India	Siddappaji & Gowda 1980
Voandzeia subterraneana (Bambarra groundnut)	*Rivellia* sp.	L	Yangambi, Democratic Republic of the Congo	Seeger & Maldague 1960

the Fabaceae, the hosts for North American species of *Rivellia* mostly appear to be members of the Papilionoideae. The subfamily Papilionoideae has the highest incidence of root nodulation (Faria *et al.* 1989). Although records are of limited extent, no larval specimens of *Rivellia* were collected from Caesalpinoideae such as *Gleditsia triacanthos* L. (honey locust) and *Cercis canadensis* L. (redbud), which produce no root nodules; but Hilty (2015) lists adults sucking nectar from *Chamaecrista fasciculata* (Michx.) Greene. Likewise, no larvae were observed in Mimosoideae such as *Schrankia nuttallii* (DC.) (sensitive brier), which do produce root nodules (Faria *et al*. 1989). Curiously, based on adult emergence numbers in field trials in North Carolina, USA, some Papilionoideae such as *Arachis hypogea* L. (peanuts) and *Phaseolus vulgaris* L. (snap bean) were not naturally infested with Soybean Nodule Fly. Clearly, a more thorough survey across the Fabaceae would elucidate the natural range of host plants.

Some degree of host specificity may exist. For example, *Rivellia melliginis* (Fitch, 1855) was observed to occur with a high affiliation for *Robinia pseudoacacia* L. (black locust tree), but not for adjacent *Amorpha fruticosa* L. (false-indigo, or bush-indigo) (McMichael *et al.* 1990), while *Rivellia micans* Loew, 1873 was only encountered on bush-indigo (Foote *et al*. 1987). Undetermined species of *Rivellia* were associated with *Glycine javanica* (pasture legume) in Australia (Diatloff 1965), while adjacent crops of other legumes such as *Vigna sinensis* (L.) Endl. ex Hassk and *Vigna gracilis* (Guill et Perr.) Hook. f. (cow peas), *Centrosema pubescens* Benth. (butterfly pea), *Desmodium intortum* (Mill.) Vib. and *D. uncinatum* (Jacq.) DC. (trefoils), and *Kennedya rubicunda* Vent. (dusky coral pea) were untouched. Likewise, in Yangambi, Democratic Republic of the Congo, *Rivellia* sp. larvae were found on root nodules of peanut, *Phaseolus aureus* (mung bean), *Vigna sinensis* (cow pea) and *Voandzeia subterraneana* (Bambarra groundnut) (Seeger & Maldague 1960), but not on *Glycine max* (L.) Merrill (soybean) and *Crotalaria longithyrsa* Baker f. (rattlepod) in the same trials.

ECONOMIC SIGNIFICANCE

The most significant of the crops associated with *Rivellia* nodule damage is soybean, *Glycine max* (L.) Merrill, which has been grown in East and South East Asia as a food crop for thousands of years, and, to this day, constitutes an important component of the traditional and popular diet in these regions. Modern production is primarily as an industrial crop, cultivated for oil and protein, accounting for 56 % of worldwide oilseed production with a market value of in excess of USD 48 billion (Wilson 2008) despite the relatively low oil content of about 20 % of the moisture component of the crop.

Among the leading producers of soybean (USA, Brazil and China), the growth has been exponential in recent years, reaching a harvested area of 73 million hectares and yielding 82,000 hectogrammes per hectare (hg/ha), or 225 million tonnes of crop (Table 3). Across the entire global market, the production comes to 128 million

Table 3. World production of soybean and specific quantities for the top three world producers.

Country	Area harvested (ha)	Production yield (hg/ha)	Production tonnes (t)	t/ha
Brazil	33,153,679	29,046	96,296,714	2.90
China	6,640,882	18,019	11,966,328	1.80
USA	33,482,430	35,006	117,208,380	3.50
Total	**73,276,991**	**82,071**	**225,471,422**	**3.08**
Global	**128,173,317**	**1,672,353**	**346,860,410**	**2.71**

hectares, 1.7 million hg/ha and nearly 347 million tonnes (FAO 2017). In China alone production increased nearly 3.5 fold in 25 years from 16.875 t/ha in 1978 to 58.5 t/ha in 2005 (Liu *et al.* 2008).

The main benefit of the crop is that, unlike other oil seeds (e.g. rape), the soybean oil meal remaining after oil extraction is valued for its commercial importance, which exceeds that of the oil. Soybean is considered by FAO as potentially one of the largest sources of human dietary protein, although at present this occurs indirectly as most soybean oil meal is used as fodder for animals producing meat and egg protein products for human consumption (FAO 2017).

Root nodule flies can significantly damage a soybean crop. Thus, *R. quadrifasciata* was reported at densities of 132 larvae/pupae per row foot of crop, damaging as much as 48 % of the root nodules (Eastman & Wuensche 1977). Newsom *et al*. (1978) noted that the impact on nitrogen fixing could be severe. In light of the dependency of the bean crops on nitrogen production by the nodules, and since nitrogen limits soybean seed, protein and oil yields (La Menza *et al*. 2017), infestation can lead to a considerable loss in production. Early planted soybean are particularly susceptible to root nodule fly attack (Eastman 1980) and plants grown in sandy-loam soils were found to be more attractive to ovipositing females. Foote (1985) postulated that highly similar chemical attributes of naturally occurring host Fabaceae enabled indigenous species of *Rivellia* to switch to introduced legume crops.

BIOLOGICAL ASSOCIATIONS AND CONTROL MEASURES

The cosmopolitan nature of the pest has resulted in varied control measures across the distribution of each host species. Consequently, the species of *Rivellia* with sufficient data available are treated individually below. There are indications that cultural practices (in the sense of cultivation methods) and application of nitrogenous fertiliser may be as effective, or better, than broad spectrum applications of insecticide. Some species of *Rivellia* co-exist on the same crop.

Rivellia angulata Hendel, 1914

Larvae frequently infest pigeon pea (*Cajanus cajan*) at the ICRISAT Center in India (Sithanantham *et al*. 1981). Sithanantham *et al*. (1987) demonstrated a positive

association between the presence of *R. angulata* and root nodule functioning. Subsequent work at the same research facility on pigeon pea and on sorghum (*Sorgorum bicolor* L. Moench) noted that root nodule damage was greater in crops grown in vertisols compared to those grown in alfisols and that there was a 70 % rate of damage to root nodules in artificially inoculated potted plants (Kumar Rao & Sithanantham 1989).

In contrast, in pulse crops in northern Karnataka, India, larvae of *Rivellia* sp. caused up to 98 % nodule damage to mung bean (*Vigna* spp.), urd (*V. radiata*), cow-pea (*V. unguiculata*), pigeon pea or red gram (*Cajanus cajan*) and groundnut when sown in July or later (Siddappaji & Gowda 1980). Reed *et al.* (1989) noted that application of large doses of insecticides to soils was not successful, nor economic, but that adding nitrogen fertilizer to soil might alleviate nutrient deficiency caused by nodule damage. Later, Nambiar *at al.* (1990) demonstrated that root nodule damage could be significantly reduced by growing pigeon pea in pots seeded with strains of *Bradyrhizobium* sp. to which *Bacillus thuringiensis israelensis* was cloned. This produced a derivative gram-negative bacteria plasmid vector that transfers across a broad-host-range by conjugative mobilization.

Rivellia apicalis Hendel, 1934 and *R. basilaris* (Wiedemann, 1830)

The species is primarily associated with soybean (*Glycine max*) in Hokkaido and Kyushyu, Japan (Koizumi 1957; Kobayashi 1981). Koizumi (1957) also noted that adult *R. apicalis* feed on aphid honeydew and are often in mixed populations with *R. basilaris*. Kurosawa and Matsumoto (1961) observed *R. apicalis*, *R. nigricans* and an unidentified species of *Rivellia* in a newly cultivated patch of soybean at Sapporo, Japan.

Rivellia apicalis was also recorded from *Vigna angularis* (Willd.) Ohwi & Ohashi (Azuki bean and common bean plants such as scarlet runner) (Suzuki & Mori 1963). Chemical controls were proposed and tested in India by Bhattacharjee (1977). In addition Sugiyama and Mochizuki (1949) and Chiku and Miyashita (1957) each list an undetermined species of *Rivellia* associated with failing soybean (*Glycine max*) crops respectively in Hokuriku and Ina, Nagano Prefecture, Japan.

R. basilaris was noted as a pest of fruit of eggplant (*Solanum melongena*) at Kangton in China (Koizumi 1957); *R.* nr. *basilaris* on soybean in Australia and New Zealand (Kogan *et al*. 1997).

Oh *et al*. (2017) reported decrease in total numbers of *R. apicalis* on both Vitamin E enhanced transgenic soybean (GM 1208-3-30) and the Williams 82 variety compared to the Seoritae, black soybean variety, suggesting that there may be variety based solutions to root nodule fly control.

Rivellia flavimana Loew, 1873, *R. metallica* (van der Wulp, 1867) and *R. pallida* Loew, 1873

These three species were associated with hog peanut (*Amphicarpaea bracteata* (L.) Fernald) in the USA (Foote 1985; Foote *et al*. 1987) and potentially co-exist having probably switched hosts from local Fabaceae (Foote *et al.* 1987).

Rivellia flavipes Hara, 1994

The species is associated with *Lespedeza bicolor* Turcz. (bush clover) in Hokkaido, Japan (Hara 1994).

Rivellia flaviventris Hendel, 1914

Briefly mentioned by Hara (1993) in a taxonomic paper, the only information is that Hara collected adults of this species from *Vigna angularis* (Willd.) Ohwi & Ohashi (Azuki bean and common bean plants such as scarlet runner) in the Nagano and Osaka prefectures of Japan. Oh *et al.* (2017) reported decrease in total numbers of *R. flaviventris* on Vitamin E enhanced transgenic soybean (GM 1208-3-30) compared to the Williams 82 variety but an increase when compared to the Seoritae, black soybean variety, suggesting that there may be variety based solutions to root nodule fly control.

Rivellia mandschurica Hennig, 1945

Associated with *Amphicarpaea bracteata* (L.) Fernald subsp. *edgeworthii* (Benth.) Ohashi var. *japonica* (Oliver) Ohashi (hog peanut), *Maackia amurensis* Rurp. & Maxim. var. *buergeri* (Maxim.) C.K. Schn. (Amur maackia) and *Pueraria lobata* (Willd.) Ohwi (kudzu vine or East Asian arrowroot) in Hokkaido (Hara 1994).

Rivellia melliginis Fitch, 1855

Adults found visiting dried flowers of black locust tree (*Robinia pseudoacacia*) in the USA (Namba 1956; Newsom 1983; Foote 1985; Foote *et al*. 1987; McMichael *at al.* 1990), usually has not been associated with root nodules yet.

Rivellia micans Loew, 1873 and *R. munda* Namba, 1956

Adults of both species were recorded by Foote *et al.* (1987) from *Amorpha fruticosa* L. (false-indigo or bush-indigo) in Oklahoma and Ohio, USA, but no further information is available.

Rivellia nigricans Matsumura, 1916

The species was first recorded associated with a newly cultivated patch of *Glycine max* (soybean) at Sapporo, Japan (Kurosawa & Matsumoto 1961), but later also noted (Hara 1994) to occur abundantly on *Pueraria lobata* (Willd.) Ohwi (kudzu vine or East Asian arrowroot) in Hokkaido and Honshu, and also in Hokkaido on *Amphicarpaea bracteata* (L.) Fernald subsp. *edgeworthii* (Benth.) Ohashi var. *japonica* (Oliver) Ohashi (hog peanut), on *Glycine max* and on *Maackia amurensis* Rurp. & Maxim. var. *buergeri* (Maxim.) C.K. Schn. (Amur maackia).

Rivellia nigroapicalis Byun & Suh, 2001

The species was collected as adults from *Pueraria montana* (Lour.) Merr. (kudzu, or Japanese arrowroot) in Korea by Byun *et al.* (2001).

Rivellia quadrifasciata (Macquart, 1835)

This species was first reported, illustrated and redescribed by Eastman and Wuensche (1977) and thereafter listed as the Soybean root Nodule Fly (SNF) being

common on soybean (*Glycine max* (L.) Merrill) in the USA (Koethe & van Duyn 1984, 1985; Foote 1985). Apparently, it is non-specific in host choice as it is also found on the root nodules of lima beans (*Phaseolus limensis* Macf.) (Koethe & van Duyn 1988).

Koethe and van Duyn (1984) demonstrated that the larvae had an 89 % survival rate on nodulating soybean plants compared to only 9 % survival on nodule-free plants. Subsequently, Reeves *et al.* (2009) experimented with nodule and non-nodule treatments by *Rhizobium* inoculation, supplementing the nitrogen required in non-nodule treatments with applications of 20-20-20 (N-P-K) fertiliser. Their results suggested that with reasonable care and plant separation, the non-nodule method of growing plants may be a reliable way to grow plants for study of female oviposition choice in *R. steyskali* or *R. quadrifasciata*.

Compared with other significant soybean pests (*Cerotoma trifurcata* (Forster, 1771), the bean leaf beetle, and *Diabrotica balteata* Le Conte, 1865, the banded cucumber beetle (Coleoptera, Chrysomelidae)), *R. quadrifasciata* damaged a greater number of nodules per plant and caused significant reductions in N_2 fixed and C_2H_4 per plant and per nodule (Hutchinson 1979) in Louisiana, USA.

Chemical controls were tested for larvae on soybean (*Glycine max*), brown-eyed crowder southern peas (*Vigna unguiculata* (L.) Walp.), 'Florigiant' peanuts (*Arachis hypogaea* L.), bush variety snap-peas (*Phaseolus vulgaris* L.) (Koethe & van Duyn 1984) and on trefoil (*Desmodium* spp.) (Foote 1985; Foote *et al.* 1987). Koethe *et al*. (1986) concluded that tillage was an ineffective control, based on the deep soil (10–30 cm) overwintering habits of SNF (also noted by Pitre and Porter (1990)). In 1989, Koethe and Duyn investigated the adult biology in fields, observing SNF feed on carrion, honeydew, bird droppings, insect frass and nectar, with females predominating on more protein-rich foods; traps baited with meat or dead insects readily attracted females, but not males, while fruit (peach), ethylene glycol and soap-water baits attracted few flies at all unless meat was added. Males were effectively trapped using yellow sticky traps.

In a list of chemical controls for soybean pests (Kohn 1990), none of the 17 compounds listed were rated for control of *R. quadrifasciata*. Ambrose (2003) discussed the effects of chemical controls on cotton pests, including *R. quadrifasciata*, although it is unknown as a pest of cotton; it was the only insect pest species, besides the study target, found in sufficient numbers to analyze and therefore considered to be an indicator of insecticidal activity. It was found that there were significant efficacy between days 1 and 4 of the acetamiprid treatment, but none within or between all other spinosad, indoxacarb, methoxyfenozide and acetamiprid treatments.

Rivellia steyskali Namba, 1956

This species was noted from panicled tick-trefoil (*Desmodium paniculatum* (L.) DC) in Northeast Ohio, USA (Foote 1985; Foote *et al.* 1987).

Rivellia variabilis Loew, 1873

The species was recorded from *Apios americana* Medikus (Foote *et al*. 1987).

Rivellia viridulans Robineau-Desvoidy, 1830

Reported from piles of rotting *Narcissus* bulbs and attracted to black locust trees (*Robinia pseudoacacia*) in the USA (Blanton 1938; Foote 1985; Foote *et al.* 1987). There is no known host plant association.

Rivellia winifredae Namba, 1956

This species was noted from the potato bean or groundnut (*Apios americana* Medikus) in Northeast Ohio, USA (Foote 1985).

Furthermore, a number of observations of undetermined species in the genus *Rivellia* were noted in the literature (Table 1), but these do little more than confirm the association that this genus has with members of the Fabaceae.

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